SPATIAL DISCRIMINATION REVERSAL LEARNING SET FORMATION IN WHITE LEGHORN CAPONS AS A FUNCTION OF GENETIC AGGRESSIVENESS AND LEVEL OF EXOGENOUS ANDROGEN

by

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INTRODUCTION

Craig, Ortman, and Guhl (1965) developed strains of chickens of high and low aggressiveness from both White Leghorn and Rhode Island Red populations. They defined aggressiveness as the ability to win initial pair contests. In an initial pair contest, two strangers are placed together in a neutral pen and allowed to settle their dominance relationship; this might occur either by a fight which one bird wins, or simply by one bird threatening the other, whom then shows submissiveness toward the aggressor. Some initial pair contests, of course, have no definite outcome; e. g., the birds might not interact in the allotted time, or a fight might not be won by either bird. In the Craig et al. (1965) study approximately 70 male birds were given ten initial pair contests; those birds in the upper and lower 10 to 15 per cent of number of contests won were selected as breeders to start the high and low strains, respectively. The first generation males were matched against unselected controls for selection purposes; but for the remaining four generations the birds were matched against each other in intra-strain comparisons for breeding purposes. Only the males were selected, but these were bred to females of the same intra-strain generation.

The interesting question arises as to whether selection for differential aggressiveness also entails selection for another trait; i. e., whether the

genes responsible for genetic aggressiveness are linked with other genes, or whether one can select for birds which will differ only in aggressiveness. One possible trait, among many, which might be confounded with aggressiveness is "intelligence," defined here as the ability to form spatial discrimination reversal learning sets.

Harlow (1959) showed that if animals are given many problems with a small number of trials per problem, the animals will come to solve problems within fewer and fewer trials as the number of problems administered is increased until animals such as monkeys solve most problems after only a single trial. He called this phenomena "learning set formation." Research summarized by Harlow (1959) showed that the speed at which animals improve and the final level of performance attained seem to be related to the standing of the species in the phyletic scale, as well as within-species variables such as age. These results led Harlow (1959) to conclude that learning set formation is a measure of an animal's "intelligence"--the faster and more complete the development of the set, the higher the animal is ranked in intelligence.

There are many different learning set techniques. One general class involves the presentation of a different set of stimulus objects for each problem rather than always using the same stimuli. Variations on object-discrimination problems include oddity, size, color, and form problems.

A second general class of learning set techniques involves repeated

discrimination reversal training, rather than object discrimination training. This technique, at least when lower mammals and sub-mammalian species are utilized as subjects, generally employs a spatial Y- or T-maze as apparatus, with the positive and negative arms or positions reversed on successive problems.

With both of the above techniques, problems can be given for a fixed number of trials, or an animal can be required to reach an arbitrary criterion of performance on one problem before another problem is given. While the shape of the learning set curve (determined by plotting per cent correct responses as a function either of trials or problems) changes as a function of all these variables, an important factor common to all variations of this method is successive interproblem improvement; therefore it is assumed that all the aforementioned techniques involve the same general processes.

Although the question of how far down the phyletic scale the ability to form learning sets extends is not settled, Warren, Brookshire, Ball, and Reynolds (1960) have shown that chickens can form learning sets when a spatial Y-maze is used with a discrimination reversal technique, and the birds are run to criterion before the problem is changed. They used a series of ten spatial reversal problems, and found that not only could chickens form learning sets but that this technique could differentiate learning set formation ability between chicks which differed in age by as little as ten

days (groups were 3, 13, 23, 33, 43, 53 and 63 days of age at the start of training).

The present study was designed to gather information on the question of whether intelligence and aggressiveness are genetically linked. Since Warren et al. (1960) were able to detect age differences in learning set ability, it was thought that this technique might also be powerful enough to detect strain differences in learning set formation.

There are no known data on the influence of aggressiveness on reversal learning set formation. Since the two strains of chickens differed greatly in terms of level of aggressiveness, it is possible that differential aggressiveness could affect their learning set formation scores. If aggressiveness does affect performance in the learning set situation, then the learning set scores would be confounded with learning ability and aggressiveness. Therefore it is necessary to include a control to measure whether or not aggressiveness affects learning set formation performance. One possible strategy would be to employ a factorial experiment, in which strains were one factor and levels of aggressiveness another factor. Allee, Collias, and Lutherman (1939) have shown that injections of testosterone propionate increases aggressiveness in chickens. Hence by injecting differential amounts of testosterone propionate it would be possible to vary level of aggressiveness, and test whether or not aggressiveness influenced learning set scores. If either (or both) the hormone factor or the hormone by strain

interaction term is significant, one cannot draw any conclusions about the effect of the respective strains upon learning set formation. If, however, both are non-significant, then one would be in a position to make inferences about whether the strains differed in intelligence, since it would seem that differential levels of aggressiveness were not affecting learning set scores. The present study employed a 2 x 3 factorial experiment with Factor A referring to the high and low aggressiveness strains of White Leghorn capons, and Factor B referring to three levels of testosterone propionate (0.0, 0.5, and 1.0 mg/day), yielding six independent groups.

METHOD

Subjects

The Ss were 24 White Leghorn male chickens of the seventh generation from the special high and low aggressiveness strains developed by Craig et al. (1965), with twelve from each strain, and four in each group. The birds were hatched at the same time in the same incubator and kept in multiple deck battery brooders until four weeks of age, whereupon they were transfered to floor pens with strains intermingled until 14 weeks of age. They were then transfered to commercial individual compartment laying battery cages, which afforded audiovisual contact, but very limited physical contact. After two weeks in the cages for Replication (Rep) 1 birds and six

weeks for Rep 2 birds on an ad lib feeding schedule, the birds were weighed and placed on the following deprivation schedule: first, they were starved for food for two days (water was always available in their home cages throughout the experiment), then given a token amount of food once each day until their weight was reduced to 80 per cent of their ad lib weight; this level was maintained for the remainder of the experiment. On the sixth day after deprivation began daily injections of testosterone propionate dissolved in sesame oil were administered. The zero level group birds were treated with a dry needle. The 0.5 mg/day birds were given 0.04 cc of a solution of 12.5 mg testosterone propionate per cc of sesame oil, whereas the 1.0 mg/day birds received 0.04 cc of a solution of 25 mg testosterone propionate per cc of sesame oil. The birds were weighed and injected approximately one hour before each day's experimental session was begun. Injection was into the breast muscle, with side of injection being alternated daily to prevent muscle soreness from developing. A one cc syringe, with a 22 gauge needle, was used for all injections.

Apparatus

A Y-maze with arms at a 90° angle was used. All parts of the maze, including goal boxes and start boxes, were 20" high. The alleys were 12" wide; the stem was 30" long, and the arms were 36" long. The individual

start boxes were 14" square, and the goal boxes were 20" square. All pieces of apparatus were painted a dark grey, and the top was covered with hardware cloth. Masonite doors, which could be raised and lowered vertically by E without entailing gross bodily movement on his part, composed the front of the start boxes and goal boxes, and were placed inside each arm two inches from the junction of the arms. Two similar clay bowls, 8.5" in diameter at the top, were in the goal boxes, with food in only one of the two bowls. The same bowl was always kept in the same goal box. A bird could not determine whether a bowl contained food until it was at the entrance of the goal box, and after the door of the arm of the maze had already been lowered behind it.

Experimental Design

Since, due to time limitations, only six birds could be run at one time, it was necessary to replicate the experiment in order to get an adequate number of birds per group. Also, it was thought desirable to measure the replication by treatment interaction effects. Hence a randomized incomplete block design (Federer, 1955, p. 229) was employed, in which three groups, each composed of two birds, were run at one time. Since this required the confounding of an orthogonal degree of freedom with time of day of running, the $A \times B_{quad}$ term was chosen for the confounding, on the basis that it would contribute the least amount of desired information of all the terms.

In order to carry out the desired confounding, the groups were designated by modulo notation (Federer, 1955, pp. 173-175). In this system, zero designates the lowest level of a factor, one the next level, two the next, etc. Hence a_0 signifies the low strain of birds, and a_1 the highs; b_0 signifies the zero mg/day birds, b_1 the 0.5 mg/day birds, and b_2 the 1.0 mg/day birds. Factor A is always written first, and Factor B second; since, in a factorial, all groups are at some level of all factors, the letters may be dropped. The three low strain groups are thus designated as 00, 01, and 02, and the three high strain groups as 10, 11, and 12. In order to confound an orthogonal degree of freedom, all groups which have a plus coefficient in the table for obtaining the sums of squares (see Table 1) for that particular term (here the A x B_{quad} term) are run at the same time, while all groups with a minus coefficient are run together at another time. Hence, for Rep 1, the groups 00, 02, and 11 were run in the morning, and groups 01, 10, and 12 were run in the afternoon. For Rep 2, groups 01, 10, and 12 were run in the morning, and groups 00, 02, and 11 in the afternoon.

Procedure

Starting on the seventh day after injections were begun, the birds were allowed to eat their daily ration in the goal box, which had been placed

Table 1

Coefficients for obtaining the sum of squares for the individual degree of freedom effects in the analyses of variance of the mean errors to criterion scores.

Source of variance	d. f.	Group					
		00	01	02	10	11	12
Treatment	5						
A	1	-1	-1	-1	+1	+1	+1
B	2						
B_{lin}	1	-1	0	+1	-1	0	+1
B_{quad}	1	+1	-2	+1	+1	-2	+1
A x B	2						
A x B_{lin}	1	+1	0	-1	-1	0	+1
A x B_{quad}	1	-1	+2	-1	+1	-2	+1

in a neutral room, for four days. On the first of these days the birds were placed directly into the goal box; on the next three days, they were required to go from their start boxes, which had been placed directly in front of the goal box, into the goal box in order to eat. On the eleventh day after the start of injections the birds were given twenty adaptation trials in the maze, with both arms containing food. On the twelfth day original learning was started, with the positive arm for each bird being the one which he had entered the least number of times on the trials of the previous day. The birds received twenty noncorrection trials per day, with the same arm positive until the criterion of at least eighteen correct choices out of twenty trials during a single daily session were achieved. On the day following the completion of original learning, reversal training was begun, in which the negative arm during original learning was now designated as positive, and the previously positive arm was now negative. After the eighteen correct out of twenty trials during a single session was again achieved, the positive and negative arms were again switched until the same criterion was met; this was continued until the birds had completed seven reversals.

The birds were run seven days a week, and were under 22 hours of food deprivation at the start of each experimental session, in addition to being kept at 80 per cent of their ad lib weight. During any daily session, all birds received Trial 1, then all birds received Trial 2, and so on throughout the session. This resulted in an intertrial interval of approxi-

mately eight minutes for each bird. The birds were kept in individual start boxes between trials in a separate room adjoining the experimental room. At the start of a trial, the bird in the start box was brought in and was placed at the end of the maze stem. The start box door was raised, and after the bird had chosen an arm the door at the entrance to that arm was lowered behind it, preventing retracing. After the bird had entered the goal box, the goal box door was lowered behind it. The bird was kept in the goal box approximately thirty seconds, during which time it was allowed access to its maintenance food if it had chosen the positive arm. At the end of thirty seconds, it was transfered to its start box, which was then transported back to the adjoining room and another bird was brought in for its trial. Although most birds consumed their daily ration of food in the experimental situation, those which had not were given enough food to complete their daily ration when they were returned to their home cages at the end of the session.

RESULTS

One bird in Rep 1 (group 11) and one in Rep 2 (group 02) died during the experiment, and two birds in Rep 2 (one each in groups 11 and 12) had to be discarded for failure to adapt to the experimental situation. This necessitated an unweighted means analysis (Winer, 1962, pp. 222-224), due to the unequal n of the various groups. The means of the cells which had only one S was substituted as a dummy value for the missing S in order to

get the same number of observations per cell (Li, 1957, pp. 209-210), and the standard computational procedures for the analysis of variance of a randomized incomplete block design was then employed. Since, however, this procedure yields inflated F values (Li, 1957, p. 210), the F values were adjusted by multiplying them by the quotient of the harmonic mean divided by the original number of observations per cell (Dr. Stanley Wearden, personal communication).

The mean number of errors to criterion over all seven reversals of the various groups are shown in Table 2, and the factorial analysis of variance of these means is shown in Table 3. The B effect (level of hormone), with two degrees of freedom, was broken down into individual degree of freedom orthogonal polynomial comparisons of linear and quadratic. The coefficients for the orthogonal polynomial comparisons were obtained from Fisher and Yates (1957, p. 90). The linear term was not significant ($p > .20$), but the quadratic term was significant ($p < .001$). In order to determine which strains were responsible for the significant quadratic effect, the quadratic component for each strain was calculated separately. The quadratic component of the high strain was not significant ($p > .20$), whereas the quadratic component of the low strain was significant ($p < .001$). This means that the significant overall quadratic effect was due entirely to the low strain.

Table 2

Mean number of errors to criterion over seven reversals for each rep and group.

Rep no.	00	01	02	10	11	12	Rep means
1	5.00	11.22	6.07	9.14	7.57	7.57	7.76
2	6.93	13.14	10.28	5.07	5.57	4.00	7.48
1 and 2	5.96	12.18	8.18	7.10	6.57	5.78	

The A x B_{lin} interaction term (strains by linear hormone response) was significant ($p < .025$), as was the A x B_{quad} interaction term (strains by quadratic hormone response, $p < .001$). In order to better understand the nature of these significant interaction terms, one must examine the hormone response curve for each strain separately. Figure 1 shows the response curve of the two strains plotted as a function of hormone level and mean number of errors to criterion. The linear term for the low strain was significant ($p < .05$), but the linear term for the high strain was not significant ($p > .10$). Therefore the statistical significance of the A x B_{lin} term was due to the fact that levels of hormone did not significantly affect the birds of the high strain in a linear fashion, whereas the low strain birds were so affected. Since time of day of running is confounded with the A x B_{quad} effect, one cannot directly determine whether the significance

Table 3

Analyses of variance[1] of the mean error to criterion scores.

Source of variance	d. f.	Mean square	F
Total	19		
Treatment	5		
A	1	31.3502	24.21***
B	2		
B_{lin}	1	0.7921	0.61
$B_{lin(o)}$	1	9.7682	7.54*
$B_{lin(1)}$	1	3.4848	2.69
B_{quad}	1	36.5054	28.19****
$B_{quad(o)}$	1	69.5642	53.72****
$B_{quad(1)}$	1	0.0417	0.03
A x B	2		
A x B_{lin}	1	12.4609	9.62**
A x B_{quad}	1	33.1004	25.56****
Rep	1	0.4134	0.32
Rep x Trt	5		
R x A	1	52.2445	40.35****
R x B	2		
R x B_{lin}	1	1.9321	1.49
R x B_{quad}	1	0.1519	0.12
R x A x B	2		
R x A x B_{lin}	1	0.7921	0.61
R x A x B_{quad}	1	2.9304	2.26
Within	8	0.9711	

1. The within term was the denominator for all F tests.

*$p < .05$

**$p < .025$

***$p < .005$

****$p < .001$

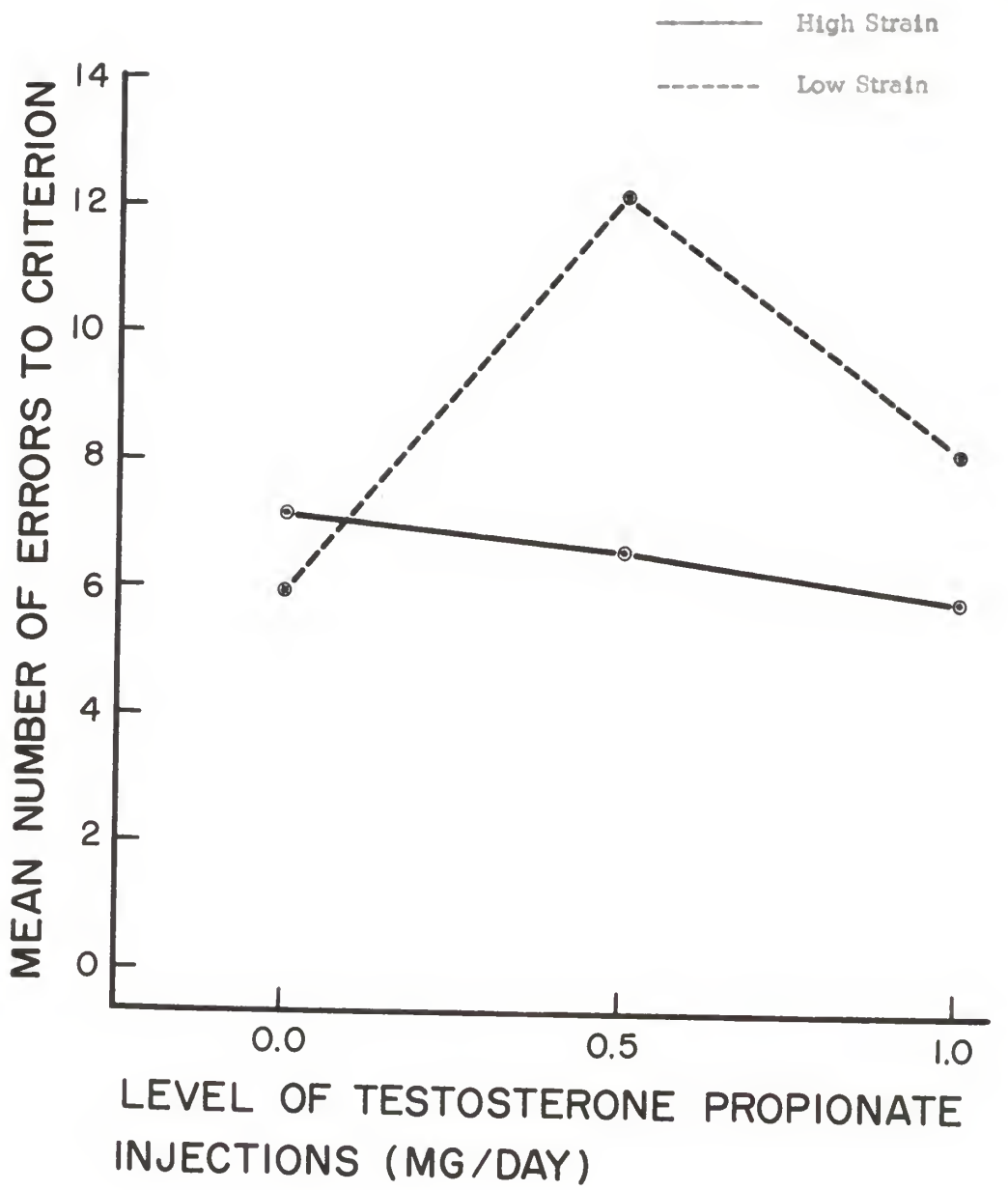

Figure 1. Mean number of errors to criterion as a function of injections of testosterone propionate.

is due to a time effect or to differential strain effects. However, since the order of the curves differ (only the low strain's response curve is quadratic, as mentioned above), it is highly likely that a direct test would have yielded significant differential strain effects. In summary, it appears that the hormone function of the low strain is mainly quadratic since the quadratic term is significant ($p < .001$), and the quadratic component accounts for 88 per cent of the variance (although the linear term was significant at the .05 level, it accounts for only 12 per cent of the variance). The effect of hormone level, on the other hand, does not have a significant influence on the high strain (neither of the B terms is significant).

The only difference other than random variability between birds in the two reps is that Rep 2 birds were approximately four weeks older than Rep 1 birds at the start of their respective experimental sessions. Qualitative observations gave the impression that Rep 2 birds appeared to be more "anxious," and to have a more difficult time in adapting to the experimental situation than the younger Rep 1 birds. This observation is further indicated by the fact that it was necessary to discard two Rep 2 birds for excessive wildness, while none had to be discarded in Rep 1. It therefore is possible that the significant R x A interaction term (reps by strains, $p < .001$) reflects a differential effect of age on the two strains.

In the light of the significant B terms, one can draw no conclusions

from the significant A (strains, $p < .005$) term regarding the respective intelligence of the strains, since the data suggests that level of aggressiveness does affect reversal learning set scores. However, one is faced with the problem of interpreting the radical effect of testosterone propionate on the low strain, while the high strain was unaffected. It might be assumed that the explanation of this finding somehow lies in the difference of the strains as regards genetic (or pretreatment) aggressiveness. There are at least two possibilities of this sort. One is that the high strain Ss were not affected because their level of aggressiveness was so high that injection of testosterone propionate had no observable effect. The data of Ortman (1964), however, contradict this supposition. He injected birds from the same strains as those used in the present experiment with testosterone propionate dosages of 0.0, 0.2, 0.4, 0.6, 0.8, and 1.0 mg/day, and found that both the high and low strains increased in total number of agonistic encounters as dosage level increased. Another possibility is that the effect of aggressiveness on reversal learning set behavior is nonmonotonic. If this were the case, then one would expect to get an orderly function when the aggressiveness level of the six groups are plotted against the mean number of errors to criterion. Figure 2 shows such a plot, with the cubic least squares curve drawn in. The aggressiveness levels were obtained from Ortman's (1964) data (mentioned above), with the 0.0 and 1.0 mg/day aggressiveness levels taken directly from his data,

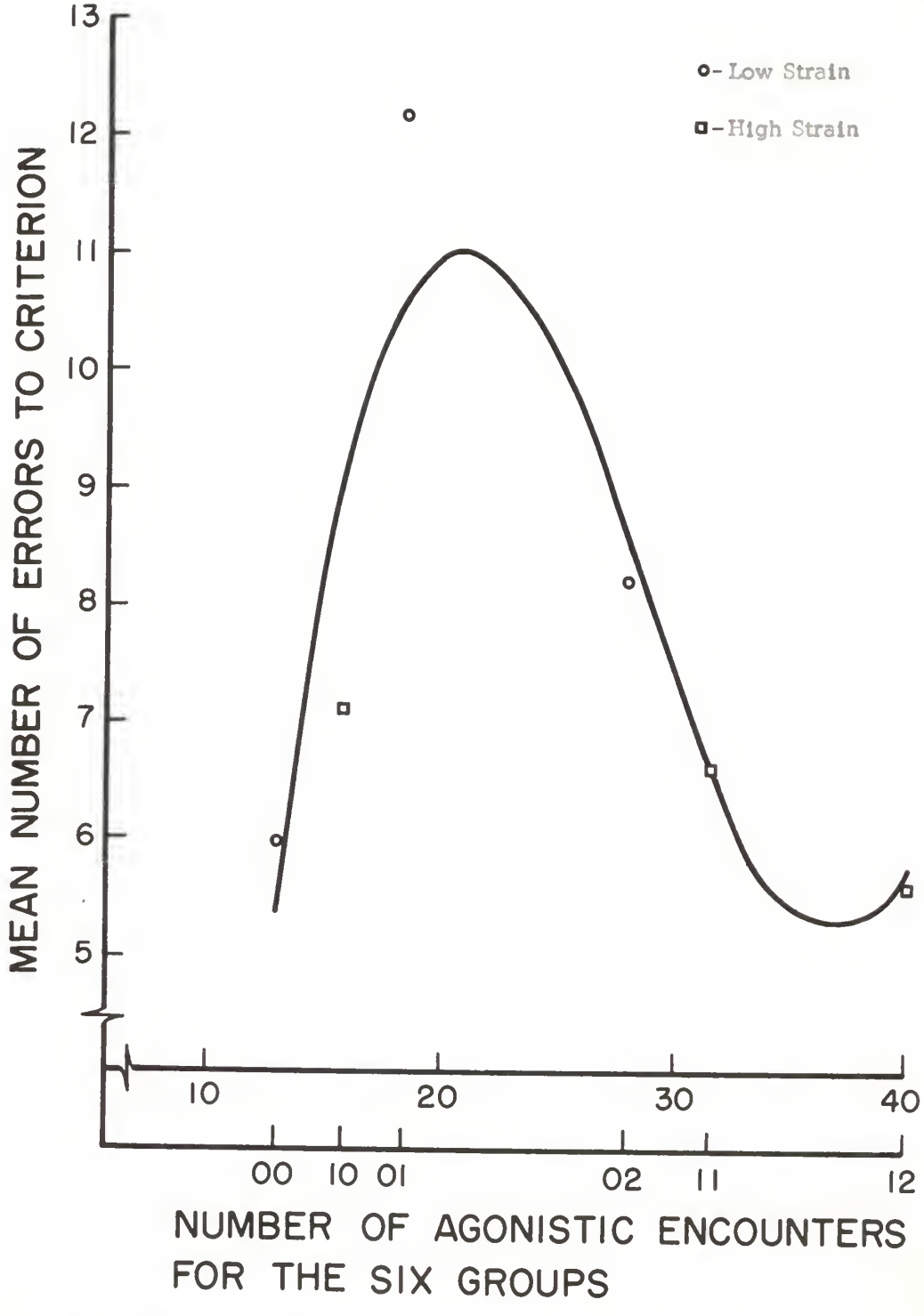

Figure 2. Mean number of errors to criterion as a function of level of aggressiveness.

and the 0.5 mg/day levels taken as the average of the 0.4 and 0.6 mg/day groups. The multiple regression analysis of variance (Snedecor, 1956, p. 452), shown in Table 4, yielded significant linear ($p < .05$), quadratic ($p < .005$), and cubic ($p < .001$) components of variance, but the quartic component was not significant ($p > .10$). The third degree polynomial

$$Y = 0.00290663X^3 - 0.25144628X^2 + 6.68781006X - 45.47343400$$

leads to an R^2 of 0.7553, and hence explains 75.53 per cent of the variance due to the six levels of aggressiveness.

Table 4

Multiple regression analyses of variance[1] of mean number of errors to criterion and level of aggressiveness.

Source of variance	d. f.	Mean Square	F
Linear	1	10.5226	8.13*
Quadratic	1	28.7826	22.23**
Cubic	1	47.1618	36.42***
Quartic	1	3.4606	2.67
Within	8	0.9711	

1. The within term was the denominator for all F tests.
*$p < .05$
**$p < .005$
***$p < .001$

Since the ordinate contains mean number of errors to criterion, it follows that the curve cannot decrease indefinitely, since one would then have birds reaching criterion with zero and even fewer errors to criterion, which is impossible. Hence, assuming a nonmonotonic curve, it must flatten out on each end, provided one samples aggressiveness levels extensively enough to reach the asymptotes. This in turn would mean that a quartic curve would be the minimum order of nonmonotonic curve possible; if a lower order curve were obtained, it would simply mean the levels of aggressiveness had not been sampled extensively enough to statistically yield the asymptotes on either one or both ends of the function. If, then, it is assumed that the true nature of the curve is quadratic, the significant cubic component simply means that the high levels of aggressiveness was sampled extensively enough to yield the asymptote on that end of the continuum.

DISCUSSION

The post hoc regression analysis strongly suggests that the function relating level of aggressiveness to reversal learning set behavior in chickens is quadratic, and that the results of the factorial analysis were due to the unfortunate choice of levels of hormone injection, which yielded aggressiveness levels in the high strain which, because of the nature of the function, yielded approximately equal error scores.

A valid test of this ad hoc hypothesis would be to run high strain birds at the injection levels of 0.0, 0.1, and 0.4 mg/day; these levels should duplicate the shape of the function obtained for the low strain in the present experiment, since they yield aggressiveness levels which approximate those of the present low strain values. If, on the other hand, the high strain still showed no effect, a true strain difference above and beyond the simple initial level of aggressiveness would be strongly indicated. Obviously, no conclusions can be drawn on this issue in the absence of further data.

It should be noted that other experimenters have found quadratic functions for the influence of variables on learning scores. Denenberg (1964) notes that the function relating emotional reactivity to avoidance learning is quadratic, as is the function relating emotional reactivity with several physiological variables. He assumes that avoidance learning is stressful, and hence motivating. Since emotional reactivity, or "anxiety" is also motivating, it follows that the same level of external noxious stimulation will have different motivating effects on Ss of different emotional reactivity. He also assumes the Yerkes-Dodson law, which states that there is an inverted U function relating performance efficiency to level of motivation, with the optimal level of motivation for a task decreasing as task difficulty increases. From these considerations he is led to predict quadratic functions for the relation of emotional reactivity with performance on tasks of moderate difficulty, since a motivation level which is too high would disrupt performance

on any but the easiest tasks.

The severe deprivation level used in the present experiment might reasonably be assumed to have a stressing effect on the birds in the present experimental situation. It therefore is possible that certain levels of aggressiveness could interact with anxiety to disrupt performance, whereas other levels might act to reduce anxiety, thereby yielding quadratic functions.

The main importance of the present findings, if confirmed by future experimentation, is to direct attention to individual, as well as group, differences in aggressiveness as a source of variability in reversal learning set formation studies with chickens. Further research is needed to determine the effects, if any, of aggressiveness on learning set formation in higher species.

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This study was conducted to determine whether or not selection for aggressiveness in chickens was independent of concomitant selection for intelligence, which was defined as ability to form spatial discrimination reversal learning sets.

High and low aggressiveness strains of White Leghorn capons, which had been selected for aggressiveness for five generations, were used as subjects.

A 2 x 3 factorial experiment, with the two strains as Factor A and three levels of exogenous testosterone propionate as Factor B, was performed. The hormone factor was included as a check to determine whether or not aggressiveness affects discrimination reversal learning set formation in chickens. Seven reversals were given in a Y-maze, with mean errors to criterion over the seven reversals as the dependent variable.

The results of the factorial analysis indicated a significant strain difference, but a significant hormone effect was also indicated for the low strain, as well as significant strain by hormone interaction terms, thereby precluding any conclusions about the respective strain's learning set formation ability. A post hoc multiple regression analysis of variance yielded significant linear, quadratic, and cubic components of variance when the level of aggressiveness of the six groups was taken as the independent variable and the mean number of errors to criterion on the seven reversals as the dependent variable. This was interpreted as

indicating a quadratic function, with the significant cubic component showing that levels of aggressiveness had been sampled extensively enough on the high end of the aggressiveness continuum to yield the asymptote.

Reference was made to the similarity of the present results to functions relating emotional reactivity and learning, which also is quadratic.